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Experimental modifications of litter supplies in a forest mull and reaction of the nematode fauna

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Summary – The reactions and behaviours of the nematode fauna in an acid mull of a deciduous forest (State Forest of Orléans, France) have been monitored for four years in the course of an experimental deprivation and doubling of annual litter supplies as well as of a deprivation of litter and rain-leaching arrivals. The deprivation of litter rapidly entails, from the year following the withholding, a regression in the density of the populations, firstly at surface (0-3 cm) then at depth (– 3-10 cm), as well as a modification in the intensity of the two seasonal activity peaks. In contrast to the other trophic groups, the density of the plant feeder nematodes increases during the two years after the litter withholding. Furthermore, a different behaviour in the animal activity at the surface and at depth occurs. As part of the two-fold litter supply, in addition to a decrease of the density of the nematode fauna, we have observed an enhancement of the dominance of fungal feeder nematodes compared to bacterial feeder nematodes, a particular trend of the level (– 1-3 cm) that behaves, in the beginning of the experiment, as a surface level (0-1 cm) then evolves like a depth level (– 3-6 cm and – 6-10 cm), thus emphasizing the surface-depth imbalance in the vertical animal distribution. Also we have pointed out an increase of the density of Cephalobidae and Plectidae contrarily to the other bacterial feeder nematodes. The experiment of litter and rain-leaching arrival deprivation has allowed us to give some elements of comparison *in situ* on the nematode resistance to a deficient soil hydric regime but also on the aptitude and rapidity of some species to react when the environmental conditions become favourable again; then the ecological significance of the behaviour of the colonizing bacterial feeder species is discussed. Referring to a previous experiment of litter supply withholding and literature data (clear-cutting, soil acidification, nematode behaviour in desert soils) the authors draw attention to the role of the litter and the underground vegetative system on the maintenance of the biological activity and on the organization of the nematode populations. Furthermore the role of these animals as potential indicators of the environmental conditions is emphasized.

Résumé – ***Modifications expérimentales des apports de litière dans un mull forestier et réactions de la nématofaune*** – Les réactions et comportements de la nématofaune dans un mull acide en forêt de feuillus (Forêt Domaniale d'Orléans, France) ont été suivis pendant quatre années au cours d'une expérience de privation et de doublement des apports annuels de litière ainsi que d'une privation des arrivées de litière et de pluviolessivats. La privation de litière entraîne rapidement, dès l'année suivant la rétention, une régression de la densité des populations d'abord en surface (0-3 cm) puis en profondeur (– 3-10 cm), ainsi qu'une modification dans l'intensité des deux pics d'activité saisonnière. A l'inverse des autres groupes trophiques, la densité des phytoparasites s'accroît pendant les deux années suivant la rétention. Par ailleurs il est noté un comportement différent dans l'activité des niveaux de surface et de profondeur. Dans le cadre du doublement de litière, en plus d'une régression des effectifs de la nématofaune, on note une accentuation de la dominance des animaux mycophages par rapport aux bactériophages, une évolution particulière du niveau (– 1-3 cm) qui se comporte au début de l'expérimentation comme un niveau de surface (0-1 cm) puis évolue comme un niveau de profondeur (– 3-6 cm et – 6-10 cm), accentuant ainsi le déséquilibre surface-profondeur dans la répartition verticale des animaux. On note également une augmentation de la densité des Cephalobidae et Plectidae contrairement aux autres nématodes bactériophages. L'expérience de privation de litière et des arrivées de pluviolessivats a permis d'apporter des éléments de comparaison *in situ* sur le comportement de résistance des nématodes à un régime hydrique déficitaire mais aussi sur l'aptitude et la vitesse de réaction de certaines espèces lors d'un retour favorable des conditions environnementales; est notamment évoquée la signification écologique du comportement des espèces bactériophages colonisatrices. Se référant à une expérience antérieure de rétention des apports de litière et des données de la littérature (coupe à blanc, acidification des sols, comportement des nématodes dans les sols désertiques), il est discuté du rôle de la litière et du système végétatif souterrain dans le maintien d'une activité biologique et sur l'organisation des populations de nématodes. Est souligné par ailleurs le rôle d'indicateurs potentiels des conditions environnementales joué par ces animaux.

Key-words : Nematoda, forest litter supplies, litter removal, hydric stress, biological indicators.

It is commonly admitted that the forest litter exerts a triple effect on edaphic populations : firstly, protection and stability of environmental conditions, particularly pedoclimatic conditions; secondly a structural role by varied habitat conditions offered to animals; thirdly an important trophic role, since about 80 % of the litter passes through the alimentary canal of invertebrates (Stachurski & Zimka, 1976), which then actively contribute to the transformation of dead organic matter, in direct and complex relationships with the microflora.

Although many studies have been carried out in forest habitats during the past twenty years in order to better understand the place and the role of free-living nematodes in food-webs (see Sohlenius, 1972, 1980; Wasilewska, 1979; Yeates, 1979, 1981; Petersen & Luxton, 1982; Ferris & Ferris, 1984), few studies have been devoted directly to the influence of the litter on the organization of nematode edaphic communities and the maintenance of a biological activity (De Goede *et al.,* 1993). Beside laboratory microcosm experiments rather showing the importance of these animals in organic matter transformation (see Vinciguerra, 1979; Coleman, 1986; Setälä & Huhta, 1990), some research studies have added insecticides or fertilizers (Santos *et al.,* 1981; Whitford *et al.,* 1982; Sohlenius & Wasilewska, 1984; Huhta *et al.,* 1986; Hyvönen & Huhta, 1989; Hyvönen & Persson, 1990; De Goede & Dekker, 1993) or have artificially acidified soils (Bääth *et al.,* 1980; Heugens, 1981; Persson *et al.* 1989; Ruess & Funke, 1992). Other analyses are relevant to sylvicultural practices such as clearing or clear-cutting (Huhta, 1976; Sundman *et al.,* 1978; Sohlenius, 1982); these practices are related to great climatic, physico-chemical and plant modifications. Experimental modifications of litter supplies, in natural conditions, seem more informative, given the progressive aspect of modification on all the functional and structural organization of soil populations. Unfortunately such studies are very rare. David *et al.* (1991) and Ponge *et al.* (1993) have recorded some work concerning the macrofauna and the mesofauna. For the microfauna (nematodes) and the mesofauna, Arpin *et al.* (1985) had carried out an experiment of litter withholding on a calcic mull; it was concluded that the role of underground vegetative systems was underestimated as compared to the litter and that the small faunal modifications they observed were attributable to this type of humus particularly rich in organic matter. A case is quoted in the literature dealing with an acid mull forest soil where the turnover of the organic matter is relatively rapid and therefore more strongly affected by the influence of annual litter supplies (Toutain & Duchaufour, 1970; Duchauffour, 1977, 1980).

This paper presents results of a field experiment carried out in a mixed forest (oak, beech, hornbeam) with an acid mull humus, where nematode fauna changes have been monitored during modifications of litter supplies.

Material and methods

The study site was located in parcel No. 921 in the State Forest of Orléans, France. The experimentation was based on three parts (Fig. 1). The first one is represented by a plot of 12 × 6 m covered by 1 m² removable square baskets made of 1 cm² plastic mesh set 50 cm above ground level. This area is divided into four parts of 6 × 3 m, each one corresponding to a treatment pursued from February 1985 to May 1989 :

1 - Plot L + H + : natural quantity of litter, herbaceous layer undamaged.

2 - Plot L + H – : natural quantity of litter, herbaceous layer (aerial parts) cut away.

3 - Plot L – H + : no litter supply, herbaceous layer undamaged.

4 - Plot L – H – : no litter supply, herbaceous layer cut away.

During 1984, sampling has been carried out on the same areas before the litter withholding started.

A second plot of the experiment has been established on an area of 4 × 4 m, some metres away from the first experiment, and has received a two-fold litter supply (plot L ++). The running experiment started in November 1985. There was a 1 m wide unsampled strip within the enclosure.

Finally in a third experiment 20 m away from the first one, both annual litter supplies and rain-leaching (plot T) were suppressed by the installation of an 8 × 4 m horticultural greenhouse (2.5 m height metallic frame covered by a plastic cloth and opened 1.3 × 1.3 m at the ends for natural air convection). The experiment also began in November 1985.

Technical points include :

1 - In every treatment baskets were emptied each week and their leaves and twigs content were turned upside down over plots L + H + and L + H –; although the litter basket arrangement was set up 8 months previously, the litter interception (taking into account the phenology of litter fall) has been effective only from autumn 1985.

2 - The size of basket meshes (1 cm²) let rain-leaching and fine organic material from the canopy pass through. On plots L – H + and L – H – the litter on the soil since the beginning of the experiment had totally disappeared by spring 1987, and on the bare soil algae and mosses grew.

3 - The herbaceous layer (*Rubus schleicheri* Weihe) was not abundant and once it had been cut regularly in 1984, it disappeared definitively within some months on experiment plots while on control plots only few shoots remained.

4 - The doubling of litter was achieved by collecting sixteen baskets covering plots L – H + and L – H – and spreading their content over plot L ++.

In each plot the sampling was carried out on five quadrats of 50 × 50 cm, twice per year (May and November). The site of quadrats was such that no point was resampled. Samples were picked up with a 5 cm diameter soil probe provided with a sharp cutting edge (Vannier & Alpern, 1968), at four depths : 0-1 cm; 1-3 cm; 3-6 cm; 6-10 cm. For each depth, the five samples were pooled. The extraction of the nematode fauna

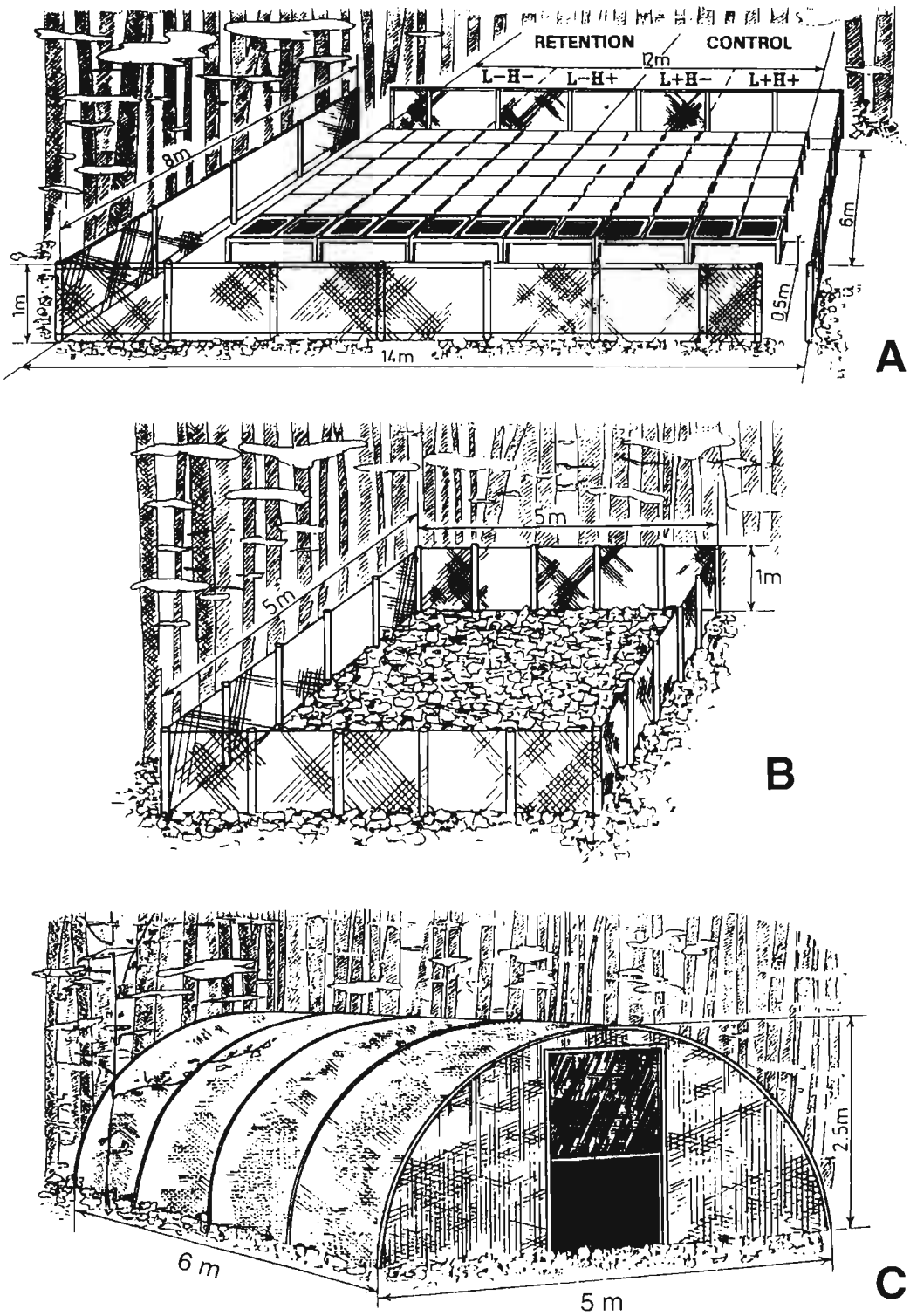

Fig. 1. *Study plots : A : Control plot (L + H + and L + H –) and plot with litter deprivation (L – H – and L – H +); B : Plot with a two-fold litter supply (L ++); C : Plot with litter and rain-leachings deprivation (T).*

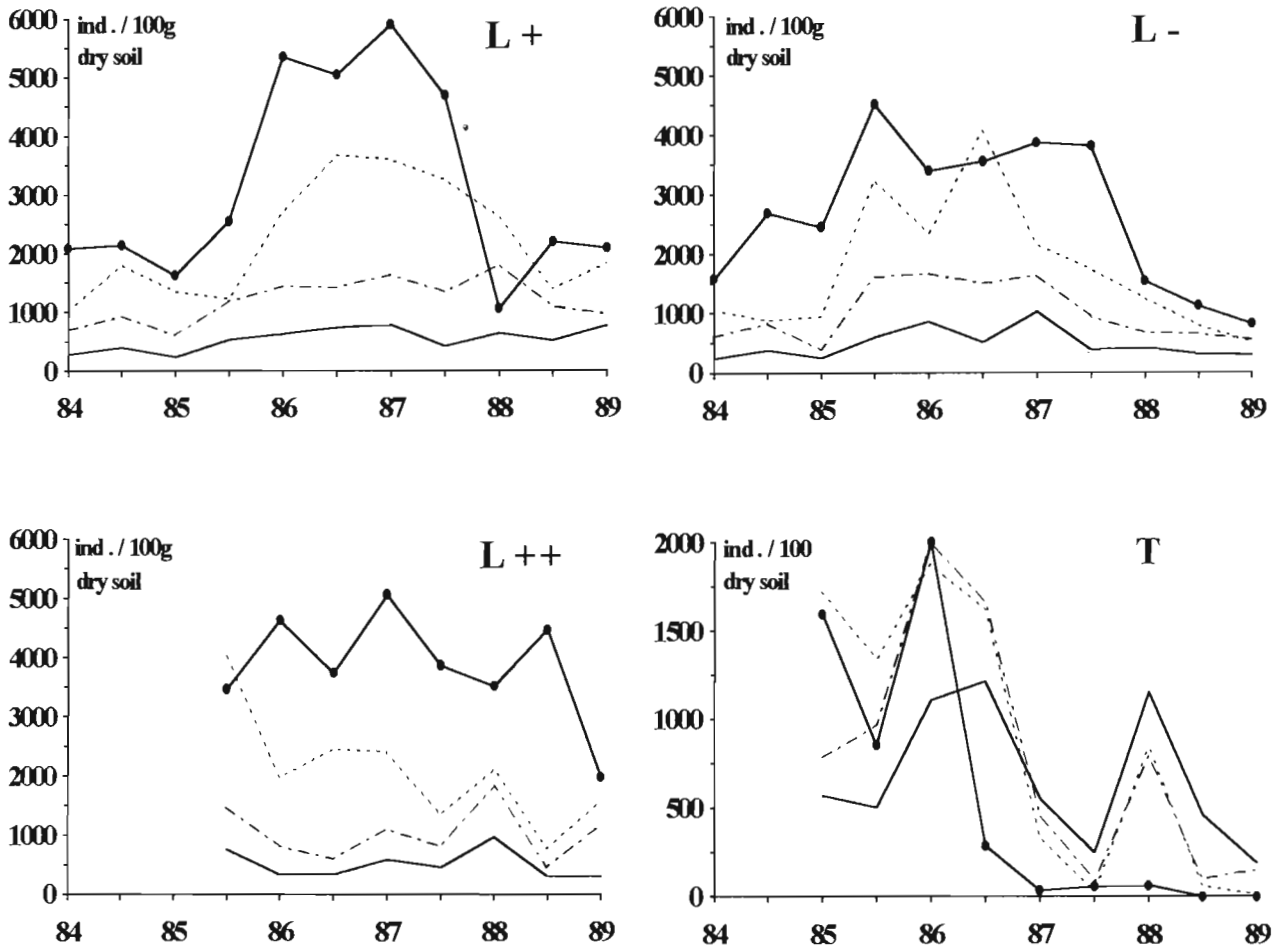

Fig. 2. *Change of the nematode density in the four plots according to the four sampling depths (•—• 0-1 cm; --- – 1-3 cm; –·– – 3-6 cm; – – 6-10 cm).*

has been processed on the whole of this pooled sample by the washing and sieving soil method (Dalmasso, 1966 as modified by Arpin, 1979). After identification and counting, nematodes were classified in trophic groups (bacterial feeders, fungal feeders, algal feeders, plant feeders, predators and omnivores) according to various classifications (Wasilewska, 1971; Yeates, 1971; Yeates *et al.,* 1993) except for *Tylolaimophorus typicus, Diphterophora communis* and to a certain extent Tylenchinae, as is discussed below.

The influence of treatments was analysed with factorial correspondence analysis (Lebart *et al.* 1979; Greenacre, 1984) on a matrix of 27 species and 244 samples. To facilitate the interpretation of graphs, we have introduced supplementary variables which do not participate in the analysis, but are plotted at the same time with species and samples (sampling depths, treatments).

Results

Natural litter supplies (plots L + H + and L + H –)

On these plots, we have collected an average of 2.4×10^6 nematodes m^{-2}, (= 7358/100 g dry soil). The change of nematode populations during the study period is represented on the Fig. 2 (L +). Densities vary substantially with time. During the first two years, individual collections in autumn ($\bar{x}$ = 5367) are more abundant than in spring ($\bar{x}$ = 3900), the reverse occurring afterwards ($\bar{x}$ = 10 374 for the spring and $\bar{x}$ = 8574 for the autumn). Similarities are observed in the evolution of the nematode fauna between depth levels 0-1 cm and – 1-3 cm, compared with deeper levels – 3-6 cm and – 6-10 cm. Subsequently, in control and litter-withholding plots, we have gathered these soil levels for better

legibility of the graphs, respectively in levels called " Surface " (75.5 % of the population) and " Depth " (23.5 % of the population). The decline of populations with depth is indicated in Table 1. If we consider the relative abundance of the different nematode trophic groups (Table 2), we can observe a slight dominance of fungal feeder nematodes (43.5 %) relative to bacterial feeder nematodes (33.5 %); this is more pronounced at the level 0-1 cm than at greater depths (Table 4). There is also a relatively important proportion of algal feeder nematodes (5.1 %).

Table 3 indicates species or trophic groups. Tylenchinae (*Tylenchus* sp., *Filenchus* sp., *Lelenchus* sp.) represent 43 % of the collected fauna; because of the conflicting literature (see Yeates *et al.,* 1993) about the feeding habits of these genera, often regarded as root/fungal feeders, and in the absence of more valuable information, we considered them as fungal feeders. *Anaplectus granulosus* (15 %), *Alaimus primitivus* (10 %) and *Teratocephalus crassidens* (3 %) are the most important bacterial feeder species (respectively 45, 30 and 9 % of this

Table 1. *Relative abundance of nematodes in the four sampling depths for each treatment.*

Levels	Treatments					
	L+	L-	L++		T	
			Before 1987	After 1987	Before 1987	After 1987
0-1 cm	46.5 %	45.5 %	50 %	54 %	23.8 %	2.7 %
-1-3 cm	30.0 %	29.5 %	32 %	22 %	32.5 %	22.7 %
-3-6 cm	16.0 %	17.0 %	12 %	16 %	26.9 %	28.3 %
-6-10 cm	7.5 %	8.0 %	6 %	8 %	16.8 %	46.3 %

Table 2. *Relative abundance of nematode trophic groups in the four sampling depths for each treatment (the difference from 100 % is due to the fact that* Tylolaimophorus typicus *is not included in a trophic group).*

Trophic groups	Treatments					
	L+	L-	L++		T	
			Before 1987	After 1987	Before 1987	After 1987
Bacterial feeders	33.5 %	25.0 %	28.6 %	32.5 %	19.2 %	34.1 %
Fungal feeders	43.5 %	43.5 %	40.4 %	56.0 %	47.6 %	45.1 %
Algal feeders	5.1 %	4.6 %	5.0 %	4.0 %	5.0 %	1.5 %
Plant feeders	5.6 %	11.4 %	15.6 %	1.0 %	17.0 %	10.5 %
Predators	1.1 %	1.2 %	0.8 %	0.8 %	0.8 %	0.2 %
Omnivorous	10.0 %	11.6 %	8.0 %	5.0 %	9.5 %	6.5 %

Table 3. *Mean densities (expressed in 100 g/dry soil) of nematode trophic groups collected on control plots (L +), plots with deprivation of litter (L -) and plots with together deprivation of litter and rain-leaching (T). (FCA code = species codes for factorial correspondence analysis; TS code = codes for trophic status of the taxa).*

Trophic groups and species	Treatments				Code FCA	Code TS
	L+	L-	T			
			Before 1987	After 1987		
Bacterial feeders	2448	1464	969	381		BF
Fungal feeders	3216	2574	2401	506		FF
Plant feeders	415	662	856	119		PF
Algal feeders	376	273	254	17		AF
Predators	80	70	38	3		PR
Omnivorous	734	678	477	71		OM
Anaplectus granulosus	1091	301	240	106	ANA	BF
Cephalobus persegnis	121	68	69	190	CEP	BF
Alaimus primitivus	737	743	440	80	ALA	BF
Rhabditis sp.	87	27	11	-	RHA	BF
Plectus sp.	87	64	84	-	PLE	BF
Teratocephalus crassidens.	224	189	45	-	TER	BF
Eucephalobus oxyuroides	76	54	80	5	EUC	BF
Bunonema sp.	20	15	-	-	BUN	BF
Diplogaster sp.	5	3	-	-	DIP	BF
Tylenchinae	3193	2563	2382	494	TYL	FF
Aphelenchoides sp.	23	11	19	12	APO	FF
Aphelenchus sp.	-	-	-	-	APU	FF
Paratylenchus sp.	59	149	568	93	PAR	PF
Criconemella sp.	210	395	211	23	CRI	PF
Diphterophora communis	113	106	77	3	DIH	PF
Longidorus sp.	22	12	-	-	LON	PF
Helicotylenchus pseudorobustus	11	-	-	-	HEL	PF
Tylencholaimus mirabilis	296	207	148	15	TYC	AF
Monhystera sp.	16	17	29	-	MOH	AF
Prismatolaimus intermedius	57	41	35	2	PRI	AF
Monhystrella sp.	7	8	42	-	MOT	AF
Mononchida	31	25	28	2	MON	PR
Trypila affinis	49	45	10	1	TRI	PR
Tylolaimophorus typicus	89	153	52	11	TLO	
Dorylaiminae	734	678	477	71	DOR	OM
Total species	7358	5874	5047	1108		

Table 4. *Mean densities (expressed in 100 g/dry soil) of nematode trophic groups and some important species for each depth sampled in control plots (L +) and plots with doubling litter supply (L ++). * : For some species in the L ++ plots, the densities before and after spring 1987 have been calculated to clearly show the decrease.*

Trophic groups and species	Treatments							
	L +				L ++			
	0-1 cm	– 1-3 cm	– 3-6 cm	– 6-10 cm	0-1 cm	– 1-3 cm	– 3-6 cm	– 6-10 cm
Bacterial feeders	1108	1139	512	236	1044	618	385	214
Fungal feeders	1652	842	539	245	2094	854	375	185
Plant feeders *	111	123	98	60	347/5	659/14	254/25	61/20
Algal feeders	163	141	71	30	133	99	73	36
Predators	34	22	10	8	33	11	9	5
Omnivorous	467	233	93	33	328	145	38	22
Anaplectus granulosus	265	719	264	147	334	336	208	133
Cephalobus persegnis	94	26	23	15	127	47	29	25
Eucephalobus oxyuroïdes	70	11	5	4	86	20	5	1
Plectus sp.	82	13	8	5	126	27	11	2
Alaimus primitivus	376	249	153	51	222	134	99	39
Rhabditis sp.	78	15	5	2	51	4	0	0
Teratocephalus crassidens	112	106	56	14	74	47	33	13
Bunonema	21	2	0	0	16	1	0	0
Paratylenchus sp. *	13	14	14	22	104/3	71/5	58/6	28/13
Criconemella sp. *	53	60	40	17	228/3	565/9	179/10	28/3
Diphterophora communis *	25	39	36	16	15/0	16/0	5/8	4/2
Tylencholaimus mirabilis	138	114	53	19	82	69	53	22
Prismatolaimus intermedius	13	24	13	8	15	21	11	7
Monhystera sp. *	8	4	4	2	72/0	11/4	14/3	12/1
Mononchida	15	9	4	3	16	3	2	1
Tripyla affinis	19	13	6	5	17	8	7	4
Tylolaimophorus typicus *	13	56	32	17	73/0	31/0	14/4	8/2

group). The Dorylaiminae (*Dorylaimus* sp., *Mesodorylaimus* sp., *Prodorylaimus* sp.) make up the essential of the omnivores. *Tylencholaimus mirabilis* and *Prismatolaimus intermedius* are the most important algal feeder species (respectively 79 and 15 % of this group). Among the plant feeders in a broad sense (grazers of plant tissues), the most representative species are *Criconemella* sp. (51 %), *Paratylenchus* sp. (14 %) and *Diphterophora communis* (27 %); although valuable information is needed, we considered here this latter species as a plant feeding nematode due to its similar behaviour to plant feeder species in our experiments (see below). Note also (Table 4) that *Tylolaimophorus typicus* is not included in a trophic group because information on its feeding behaviour is poor; it mainly occurs at deep levels (– 3-6 cm) at the limit of organic matter-mineral matter, as previously observed by Arpin and Ponge (1986).

Effects of perturbations

Results from the factorial correspondence analysis on the whole data are presented in Fig. 3, using axes 1 and 2 which extract the maximum information (30 % of total variance). Plots on the charts representing the L + H + and L + H – treatments and those representing L – H + and L – H – are respectively very closely related. Thus, the cutting of the herbaceous layer has had little influence on the behaviour of the populations. The herb layer, not very developed at the beginning of the experiment on all the plots, disappeared very rapidly during the first year of cutting, and only few shoots remained on L + H + and L – H +, so that there is no difference between treatments. Accordingly, plots L + H + and L + H – have been grouped under the label L + (control plot), and plots without litter supply will be called L –.

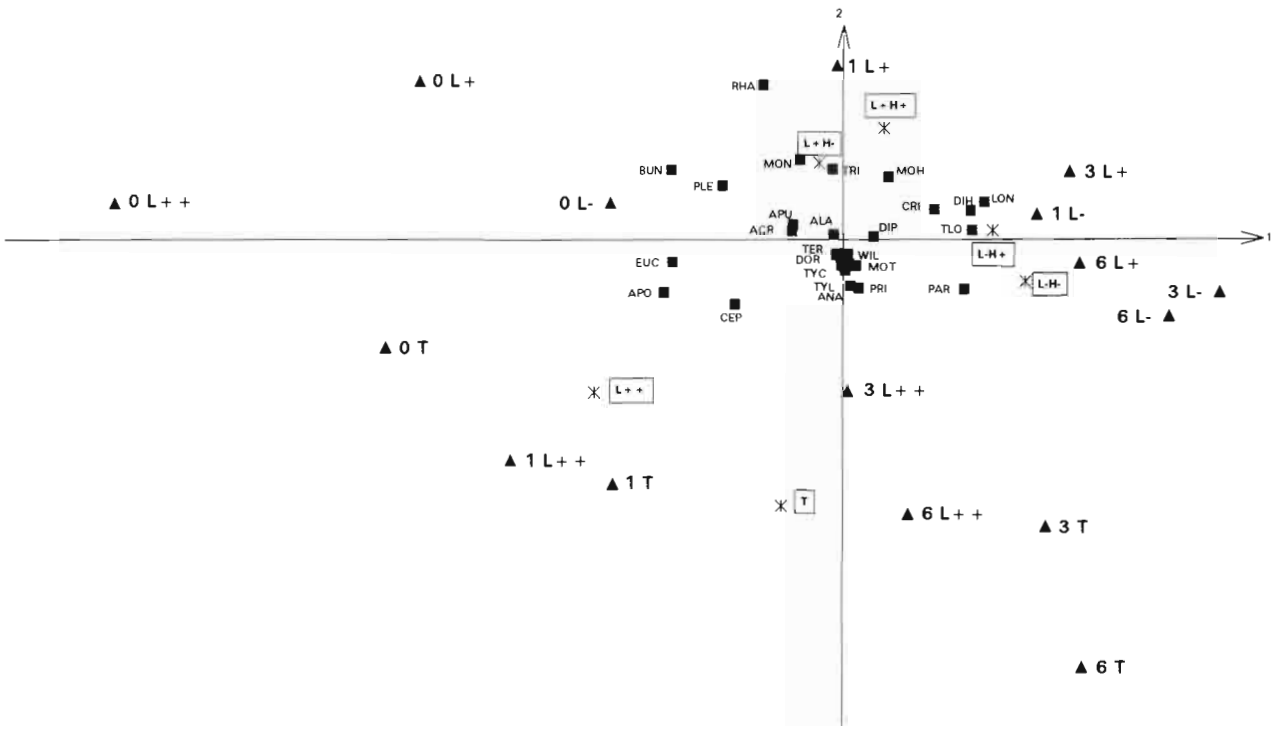

Fig. 3. *Factorial correspondence analysis (axes 1 and 2), crossing 244 samplings and 27 nematode species (for species codes, see Table 3). Treatments (*) L + H +, L + H –, L – H +, L – H –, L ++, T and sampling depths (▲) have been put in as supplementary variables according to the code : 0,1,3,6 L + respectively depth 0-1 cm, – 1-3 cm, – 3-6 cm, and – 6-10 cm of the plot L +.*

Axis 1 of Fig. 3 can be easily interpreted as an axis of animal vertical distribution, with a clear separation of the surface levels (0-1 cm and – 1-3 cm) and a tendency towards the regrouping of the depth levels (– 3-6 cm and – 6-10 cm). It is more difficult to give a precise meaning to axis 2 which seems to be related to both depths and treatments. However, several points can be noted. First of all, there exists a discrepancy between plots L + and L –, at all sampling levels, which is however more marked at the surface. The level – 1-3 cm (1 L –) in the plots L – tends to behave like the deeper levels – 3-6 cm and – 6-10 cm (3 L +, 6 L +, 3 L –, 6 L –). *Criconemella* sp. *Tylolaimophorus typicus* and especially *Paratylenchus* sp., depth species, show a decrease in their densities following the deprivation of litter (Table 3). Furthermore, in marked opposition with the control plot (L +), we find plots L ++ and T which show similar reaction to treatments nevertheless very different : practically this seems due only to the behaviour of *Cephalobus persegnis* and *Paratylenchus* sp. We can also remark, in the two-fold litter supply plot (L ++), a tendency towards a marked emphasis of the characteristics of the level 0-1 cm (OL ++) as compared to the other three depth levels and a displacement of the depth levels to the negative values of axis 2, particularly marked for the level – 1-3 cm (1 L ++). Finally, if we consider the experiment without litter supply and without rain-leaching (T), we can observe a difference in the characteristics of the two " Surface " (0-1 cm and – 1-3 cm : 0 T and 1 T) and " Depth " levels (– 3-6 cm and – 6-10 cm : 3 T and 6 T), the latter better characterizing this plot.

Factorial correspondence analysis gives a clear picture of the overall effects of perturbation of litter supply on soil nematode communities. Based on correlation and variance analysis, FCA allows detailed analysis of the behaviour of the nematode populations which are behind this differentiation.

Effects of litter deprivation

The change of density of the nematode fauna is approximatively similar on plots L + and L – (Fig. 4). However, in L –, after a short and rapid peak in November 1985, after the litter basket installation, and a second one in November 1986, we observe a constant decline of populations. On this plot, we have collected an average 5874 ind./100 g dry soil, which represents a reduction of 20.5 % as compared to the control plot. It is on the " Surface " levels that the litter deprivation produces the most effects on the total population (– 22 %) and appears from spring 1986 (– 34 % from this date). Moreover, at depth, the density of the nematode fauna re-

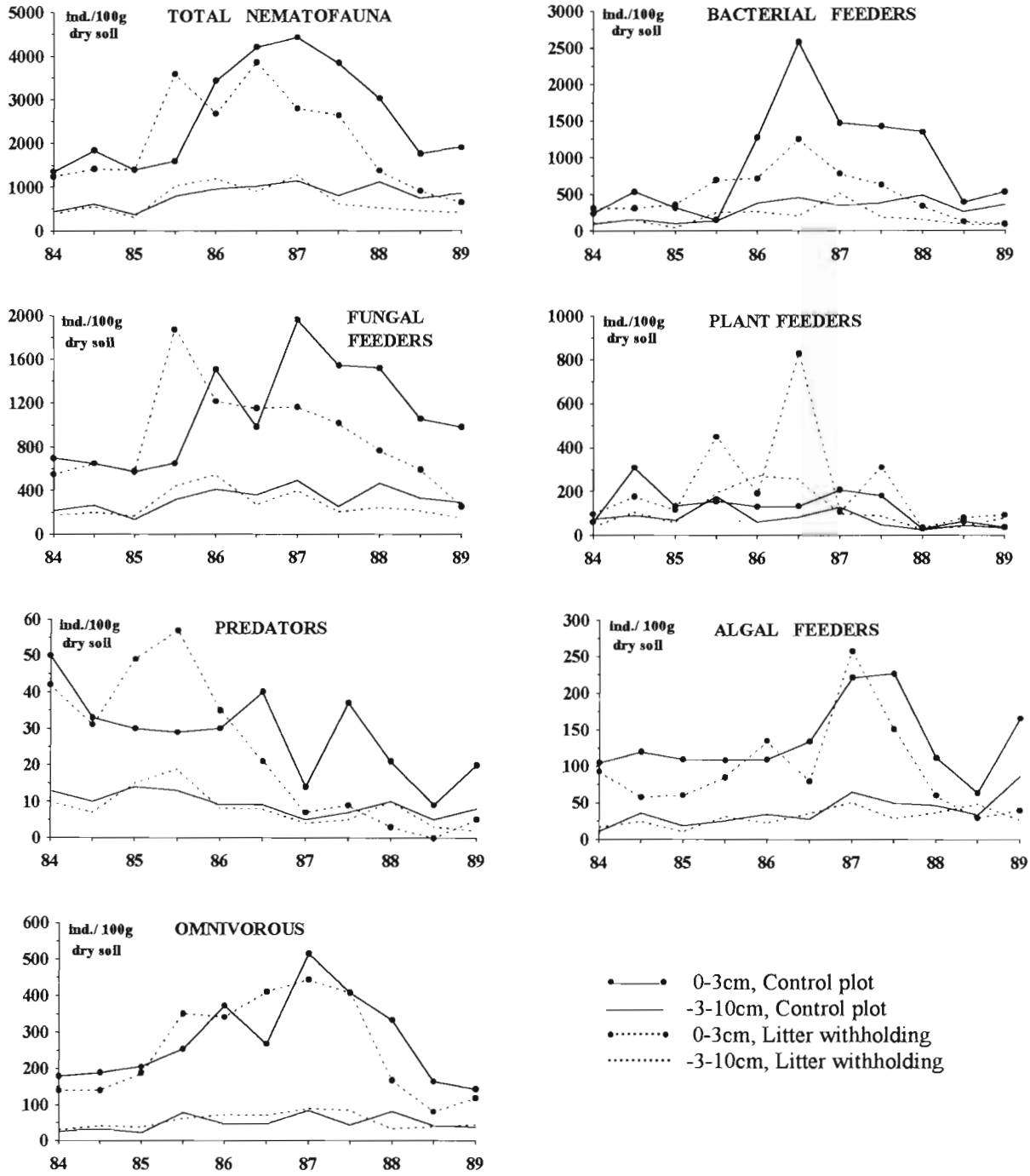

Fig. 4. *Change of the density of the nematode fauna (total fauna and trophic groups) in control plot (–) and plots with litter deprivation (----); for 0-3 cm lines have (•) and for – 3-10 cm lines have not (•).*

mains until the autumn of 1987 then a decrease of population occurs in the plot L – (– 29 % of the total collected fauna and – 43 % from autumn 1987). Furthermore, considering the four sampling depths, in the plot L –, spring collections show a deficit while autumn collections are more abundant than in the plot L +. Thus, in L +, 52 and 48 % of the nematodes are respectively collected in spring and in autumn, while 45 and 55 % are

collected in the experimental plot L – for the same periods.

Except for algal feeder and omnivore animals, which do not show notable differences between plots L + and L –, the other trophic groups react to the treatments in different ways (Fig. 4). In L –, bacterial feeding nematodes, fungal feeders and predators undergo a significant regression in their densities (respectively – 40, – 20 and – 24 % of the total collected trophic group), a process that begins in spring 1986 (respectively – 52, – 53 and – 48 % from this date). Plant feeding nematodes increase their densities from autumn 1985 to autumn 1987 on plots L – (+ 95 %). This phenomenon is particularly sensitive each autumn, with peaks very marked in the plots without litter (L –). However, if the plant feeder densities decrease afterwards, they nevertheless remain higher than in the control plot L + (+ 61 % of the total population). Generally speaking, " Surface " levels especially reveal important gaps. However, the decrease of densities of the bacterial feeding nematodes is also emphasized at depth (– 52 % at the surface and – 25 % at depth for the collected populations, and – 56 % from autumn 1986 and – 65 % from autumn 1987 respectively for " Surface " and " Depth " levels). For the fungal feeders, the regression of densities is practically identical between the two sampled depths, respectively – 19 and – 15 % for " Surface " and " Depth " (– 38 % from autumn 1986 for the surface and – 39 % from autumn 1987 for the depth). For the plant feeders, the increase is recpectively + 72 and + 51 % for " Surface " and " Depth ". For the predatory nematodes, the decrease of densities in L – is particularly strong from the spring of 1986 for the " Surface " levels, becoming even inferior to those of " Depth " levels from the autumn of 1987 (– 17 and – 12 % of the collected trophic group respectively for " Surface " and " Depth ", but – 43 and – 25 % respectively for the two sampling depths from spring 1986). Considering the change of species densities (Fig. 5), *Anaplectus granulosus, Cephalobus persegnis* and to a lesser extent *Teratocephalus crassidens* as a whole behave as bacterial feeding nematodes. On the other hand, the density of *Alaimus primitivus* decreases only from autumn 1987. Among the plant feeders, two types of specific reaction can be noted : *Criconemella* sp. and *Paratylenchus* sp. increase their densities, especially at the surface, while *Longidorus* sp. undergoes a diminution of half of its individuals (Table 3). For *Diphterophora communis,* we shall note an increase of density from autumn 1985 to spring 1987, as for the plant feeder species, then a decrease of populations whose density in L – is inferior to that of L + (opposite phenomenon to the other plant feeding species). For the two predatory groups, if a decrease in " Surface " is observed from 1986, Mononchida also undergo a decrease in depth from autumn 1987, while *Tripyla affinis* shows no change for this level. Finally for *Tylolaimophorus typicus* we observe, after litter deprivation, a sensitive increase of their densities from spring 1986 to spring 1988, mainly in " Surface " : having a marked preference for depths – 1-3 cm and – 3-6 cm in the plot L +, this species marks a preferential depth change (0-1 cm) in experimental site L –.

Effects of litter doubling

From autumn 1985 to spring 1989, the number of nematodes collected on the plot L ++ is approximately 12 % inferior to that of the control plot L + (respectively 8495 and 7458 ind./100 g dry soil) : it is mainly due to a weaker density until spring 1988, because afterwards, densities on the two plots are practically identical [Fig. 2 (L + and L ++), and Table 4]. One of the main effects of these two-fold litter supplies is the particular change of the depth-1-3 cm; from spring 1987 it takes the characteristics of a depth level (– 3-10 cm). This phenomenon does not appear in the control plot (Fig. 2 L+). Furthermore, the predominance of the surface level (0-1 cm) as compared to the other sampling depths is more emphasized on the plot L ++ than on L +, especially after 1987 (Table 1).

As for the bacterial feeding nematodes, the difference of density observed between L + and L ++ (Table 4) is weak for the depth 0-1 cm (– 6 %), stronger at – 3-10 cm (– 20 %) and very large for the depth – 1-3 cm (– 46 %). However, the density of this trophic group varies as the experiment proceeds (Fig. 6) with a notable peak of densities in autumn 1986 (depth – 1-3 cm), a peak in autumn 1987 (depth 0-1 cm) and a peak in spring 1988 (depth – 3-10 cm). Bacterial feeding species, on the whole, follow this change, especially a density decrease in the depth – 1-3 cm. However, we note an opposite behaviour for Cephalobidae (Table 4) : *Cephalobus persegnis* and *Eucephalobus oxyuroides* show a large increase in their densities (respectively + 47 and + 26 %) at all sampling depths, particularly at – 1-3 cm. It is the same for *Plectus* sp. (+ 55 %). Finally we note a global decrease (– 38 %) for *Anaplectus granulosus,* which especially occurs at the depth – 1-3 cm and in deep zones, while at 0-1 cm this species is more abundant (+ 26 %).

As for the fungal feeding nematodes, we observe a decrease of densities at depth (– 28.5 %) while at the level 0-1 cm it clearly increases (+ 27 %) and at the level – 1-3 cm there is no change (Table 4). Furthermore this plot L ++ emphasises the dominance of the fungal feeding animals as compared to bacterial feeding nematodes (Table 2).

As for the predatory nematodes, there is a decrease in densities as compared to the control plot, marked for all the sampling depths and mainly for depth – 1-3 cm (– 46 %). As for the trophic groups as a whole, the surface level 0-1 cm presents a varying nematode density while the depth – 1-3 cm behaves as a depth level from the beginning of the experiment (Fig. 6). The lesser decrease of *Tripyla affinis* (– 16 %) as compared to

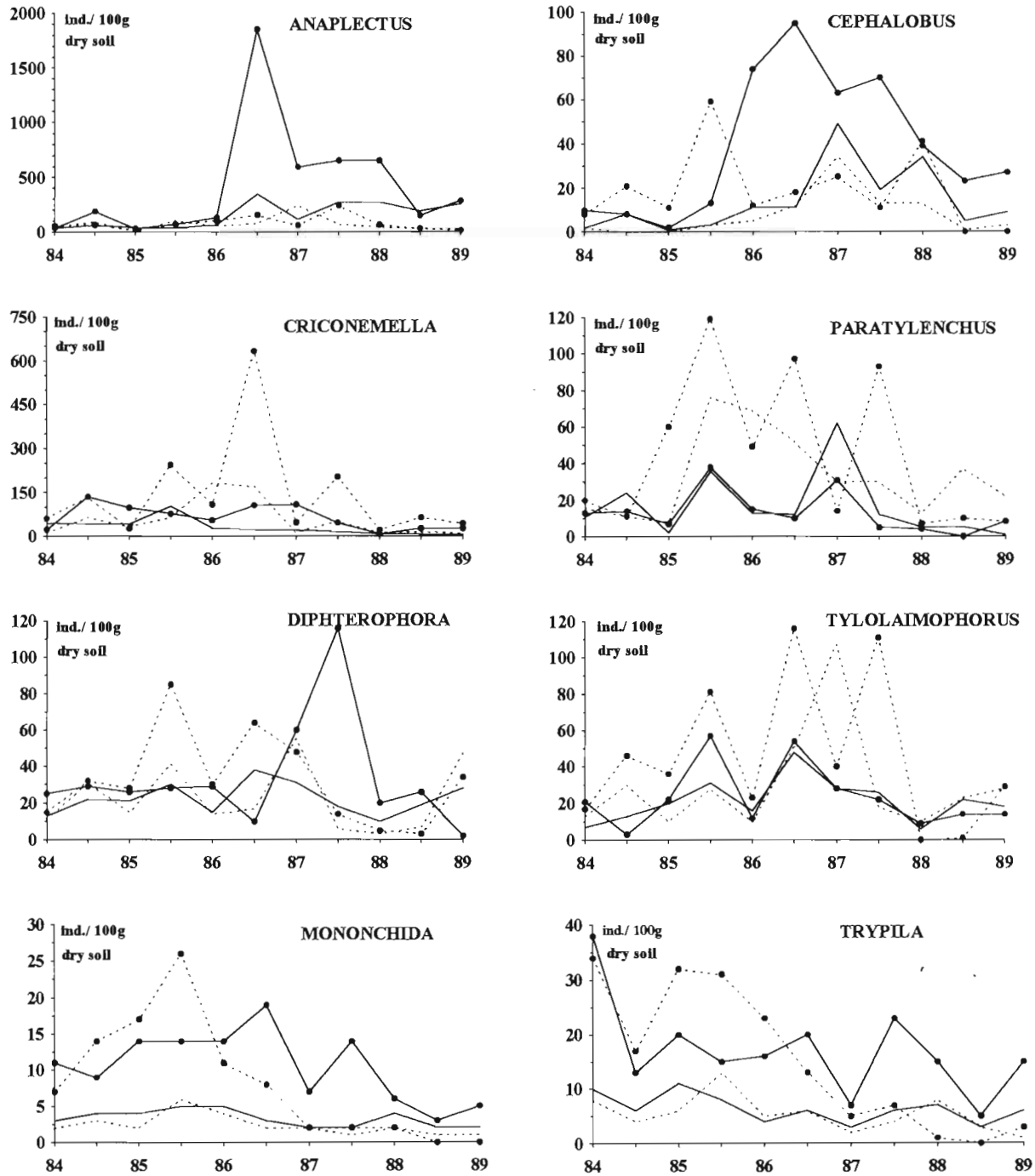

Fig. 5. *Change of the density of some characteristic genera in the control plot and plots with litter deprivation (see legends in Fig. 4).*

Mononchida (– 28 %) is due to a better maintenance of this species in the sampling depths, – 3-6 cm and – 6-10 cm (Table 4).

We find a similar decrease for the algal feeder and omnivore nematodes. As for the plant feeding nematodes (Fig. 6), although the densities at the beginning of

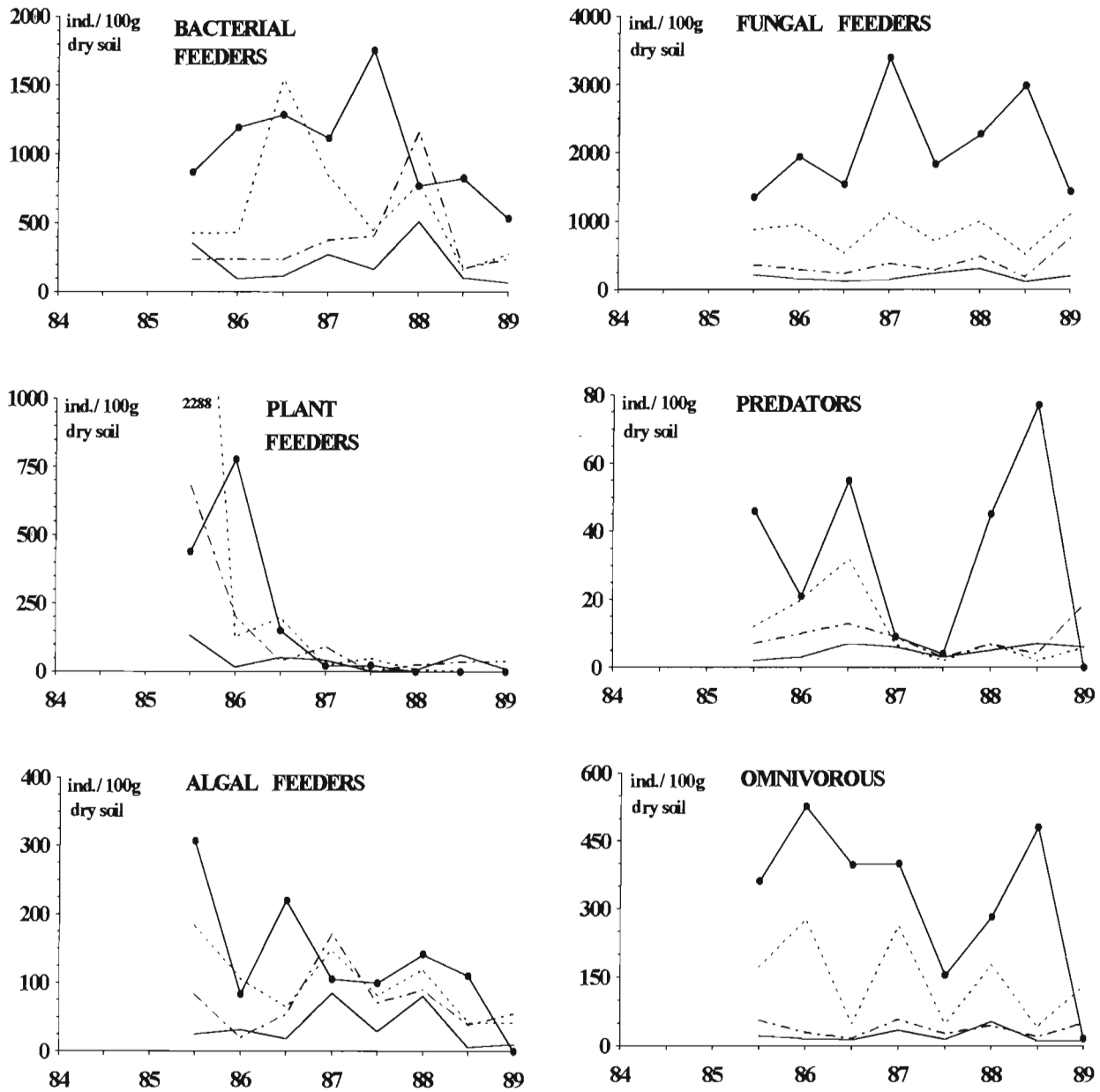

Fig. 6. *Change of the density of the nematode trophic groups in the two-fold litter supply plot : (•— depth 0-1 cm; --- depth – 1-3 cm; –·– depth – 3-6 cm; — depth 6-10 cm).*

the experiment are clearly greater in plot L ++ than in L + (Table 4), we note a much emphasized global decrease in the surface, with a disappearance of animals from spring 1988 at the depth 0-1 cm. The behaviour of these nematodes therefore seems opposite to that observed during the withholding of litter (increase of densities).

Effects of litter removal and rain-leaching arrivals

Owing to the removal of rain-leaching arrivals and the practical impossibility in forest to compensate the soil moisture loss, this plot is marked by a gradually deficient water regime. The only sources of humidity for the soil

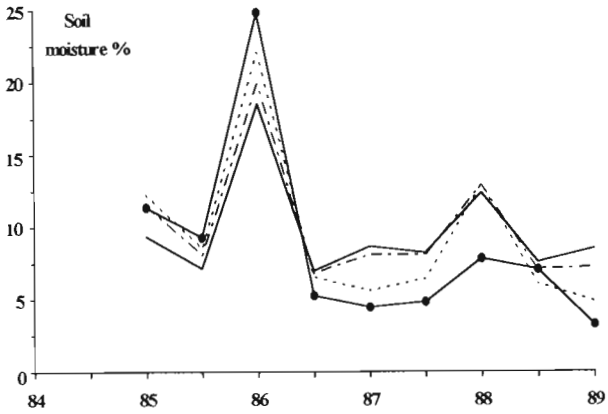

Fig. 7. *Change of the soil moisture in plot T : (•—• depth 0-1 cm; --- depth – 1-3 cm; –·– depth – 3-6 cm; — depth 6-10 cm).*

are the capillary ascents due to the variations of ground water level. We observe notably two spectacular ascents in springs 1986 and 1988 (Fig. 7). We can note that, from autumn 1986, pF 4.2 is reached for the surface levels (pF 4.2 for 0-1 cm = 9.2 %; for – 1-3 cm = 6.8 %; for – 3-6 cm = 5.5 %; for – 6-10 cm = 4.9 %). Furthermore, we observe in autumn 1986 an inversion in the soil moisture for the different sampling depths which did not change right up to the end of the experiment in spring 1989.

The population graphs of the total nematode fauna (Fig. 2), with a lower density than in the control plot, reproduces the change of the soil moisture (Fig. 7), with notably the two peaks of springs 1986 and 1988 and a tendency towards a decrease of densities clearly emphasized during the time. All the sampling depths behave in a similar way over the time, except for the depth 0-1 cm where the number of nematodes collected is practically zero from spring 1987. From this time, the only collected nematodes in the surface were these of the depth – 1-3 cm. Secondly, we observe in spring 1987 an inversion in the dominance order of the sampling depths, corresponding to the soil moisture inversion in autumn 1986. Thus, the peak of densities in spring 1986 is mainly due to animals living in the surface levels (0-3 cm) and the one in spring 1988 to animals living in deeper zones (– 3-10 cm).

Generally speaking, the trophic groups present the same change, except for the algal feeder nematodes, the omnivorous and the predators, whose densities strongly decrease from the beginning of the experiment (Fig. 8). However, some specific behaviours are interesting to analyse. Among the bacterial feeding nematodes, we can note three behaviour types (Fig. 9, Table 3). Non-resistant species disappear rapidly from autumn 1986 or spring 1987, such as *Teratocephalus crassidens, Plectus* sp. and *Rhabditis* sp. More resistant species, despite a decrease of their densities, maintain a certain capacity of response to the hydric stress, such as *Eucephalobus oxyuroïdes, Alaimus primitivus* and especially *Anaplectus granulosus* (depths – 3-6 cm and – 6-10 cm). Finally there exists a very resistant species, *Cephalobus persegnis,* whose explosive development, in " Surface " as well as in " Depth " in spring 1988, not only expresses its capacity of tolerance to the dryness, but also and especially its aptitude to rapidly react when the medium conditions become favorable again; this confers to *Cephalobus persegnis* a great capacity of colonization. We find among the fungal feeders Tylenchinae the same behaviour as for Cephalobidae. There is a disappearance of the algal feeder nematodes, except for *Tylencholaimus mirabilis* responsible for the peak of 1988, but the densities remain weak. Furthermore, *Tylolaimophorus typicus,* in general a depth species (– 3-6 cm), maintains its densities on this plot : their density peak in autumn 1988 (while all other the species show a maximal density in spring 1988 after the rehydration of the soil layers by capillary ascent) is a revealing phenomenon, because we can observe the same evolutionary tendency in the control plot (compare Figs 5 and 9) where hydric conditions are compatible with the development of these animals. Finally, among the plant feeding nematodes where we note the disappearance of *Longidorus* sp. and *Helicotylenchus pseudorobustus,* non-frequent species in the control plot (Table 3), we can also observe two behaviour types (Fig. 9). Some species, abundant in " Surface " in the control plot, are not very drought resistant species such as *Criconemella* sp. and *Diphterophora communis,* where only some individuals are present in " Depth " at the end of the experiment. On the other hand, *Paratylenchus* sp. (depth species on the control plot) is very resistant and its density increases strongly in springs 1986 and 1988.

Finally we must emphasize an identical behaviour for the drought resistant species with a strong colonizing capacity (*Cephalobus persegnis, Paratylenchus* sp, *Tylolaimophorus typicus*) : they show, especially in spring 1988, a higher peak of density than we can collect at the same period in the control plot (compare Figs 5 and 9).

Discussion

Before analyzing the reactions of the nematode populations to induced perturbations in litter supplies, it is interesting to emphasize some aspects of the behaviour of these animals in the control plot L +.

Natural litter supplies

If the density of the nematode populations ($\bar{x}$ = 2.4×10^6 ind m^{-2}, varying from 1.1 to 4.1×10^6 ind m^{-2}) is in accordance with the range of variability observed in deciduous forests in temperate zone (Sohlenius, 1972, 1980; Yeates, 1979, 1981; Petersen & Luxton, 1982), the progressive abundance regression with the depth

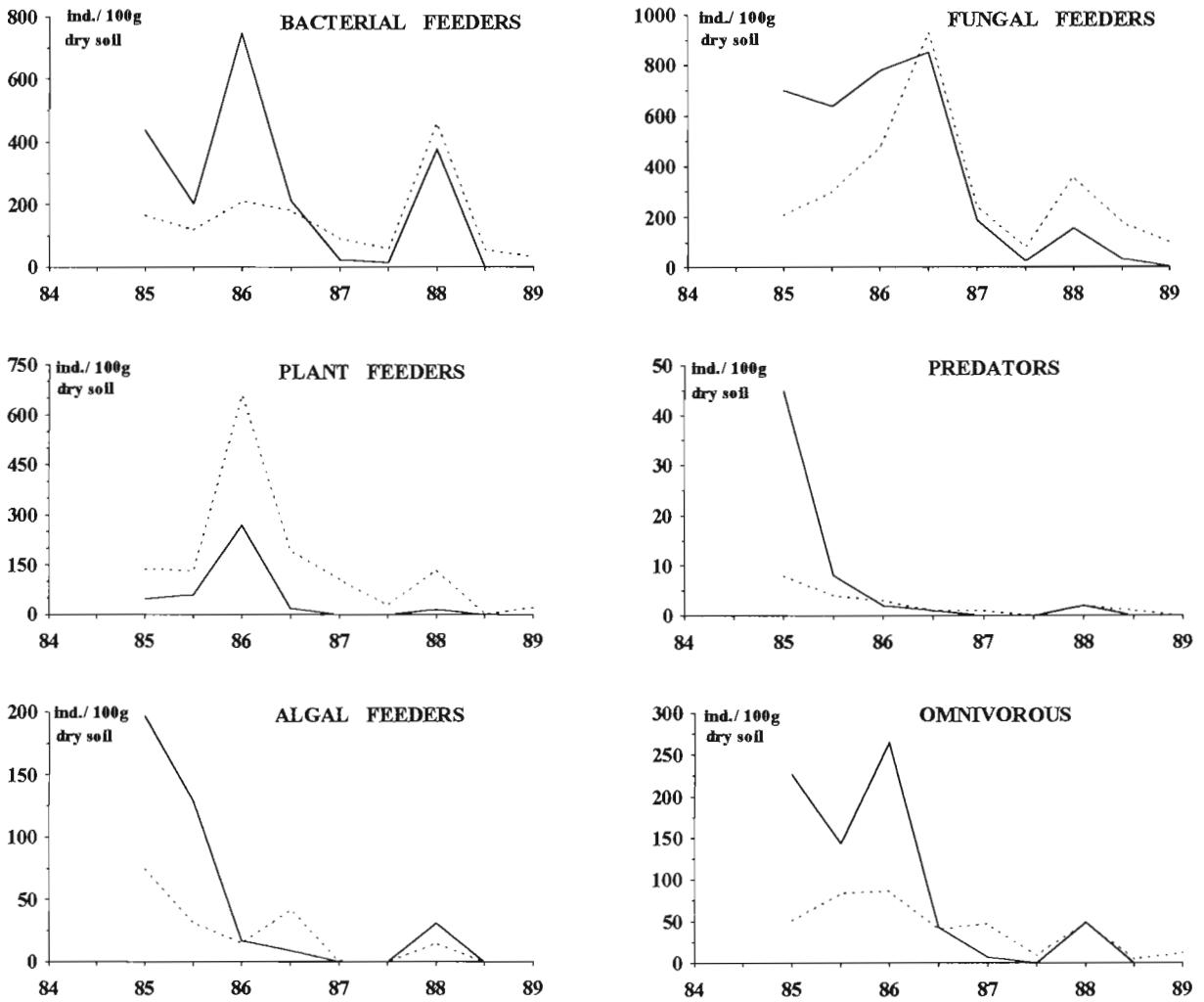

Fig. 8. *Change of the density of the nematode trophic groups in the litter and rain-leaching deprivated plot (– depth 0-3 cm; ---- depth – 3-10 cm).*

actually shows the existence of a typical mull humus. However, the weak dominance of the fungal feeding nematodes as compared to bacterial feeder species expresses both a soil acidity (pH = 5.2) and more hyphal decomposition of the organic matter. Furthermore, given the relatively high abundance of bacterial feeder nematodes, we can conclude for a correct bacterial activity of this soil (C/N = 13.2, organic matter rate of the horizon A 1 = 3.3 %; David *et al.*, 1991). We have indeed a typical acid mull humus. The soil acidity is also emphasized by the presence of *Tylolaimophorus typicus*, acidophilic species generally located at the boundary between the organic and mineral levels. Furthermore, the relatively high number of algal feeder nematodes accentuates the wet condition of this soil, with a permanent water-table at 1 m depth and temporarily near the surface (– 14 cm) during the rainy winters. These observations are entirely in agreement with previous analyses carried out in the same forest (Arpin & Ponge, 1986).

It is not easy to explain the seasonal periodicity observed on the population graphs (Fig. 2) with an autumn dominance in the first two years then a spring dominance. It may simply reflect the actual sampling. Arpin *et al.* (1985) in particular, although noting a spring peak prevalence, had displayed small variations according to years in the appearance of the activity peaks of the nematode fauna, samples occurring every two months for five years. Moreover, Twinn (1974) and Arpin *et al.* (1985) have described successive seasonal waves of activity during the year for the different trophic groups as well as for the species within these groups. Here, with only two samples a year, we are surely at the

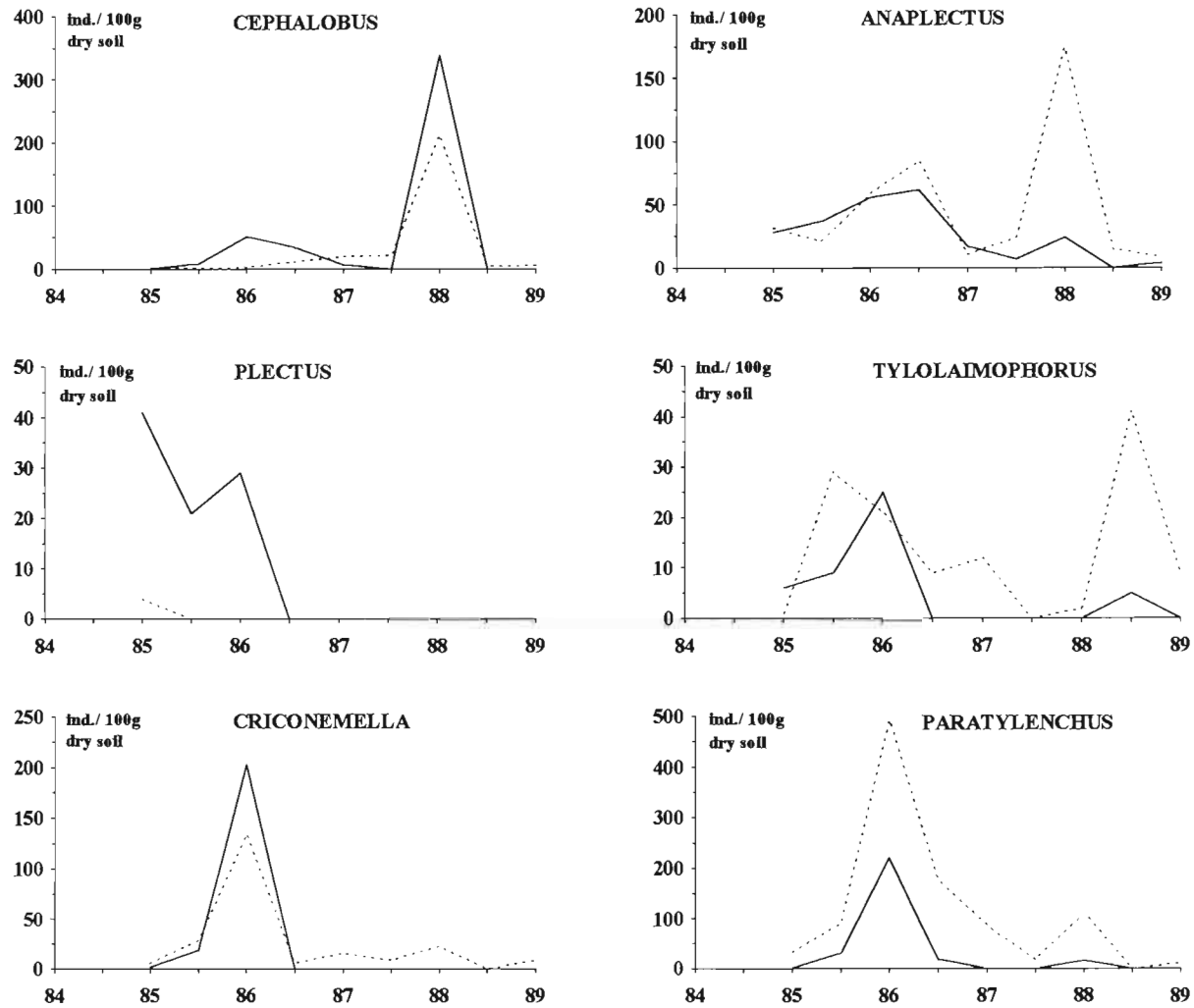

Fig. 9. *Change of the density of some characteristic genera in the litter and rain-leaching deprivated plot (see legends in Fig. 8).*

beginning or in the growth phase of the populations, which could have explained the seasonal dominance difference depending on the year. However, in this plot L +, with identical samples, the macrofauna always presents a higher density in spring than in autumn (David *et al.,* 1991). Does the seasonal change observed among the nematodes reflect more an activity of the nematode fauna in relation to this humus type (no organic matter accumulation and very rapid turnover), these animals being very sensitive to perturbations, according to the year, in the qualitative and quantitative arrivals of mineral and organic elements to soil? In an experiment of litter withholding cited above (Arpin *et al.,* 1985), authors had displayed a discordance in the appearance of the density peaks, autumn densities being higher in the plot without litter supplies, the populations rapidly reacting to easily assimilated trophic supplies especially due to rain-leachings. We find elsewhere an identical phenomenon in this work. Wasilewska (1971) also showed a variation of the density peaks of the nematode fauna in relation to the degree of dune plant cover : autumnal peak is manifest for the afforested zone, then autumnal and spring peaks are equivalent in the 10-year-old pine zone, finally spring peaks dominate in complex zones of plant cover.

Effects of litter supply suppression

The results of the factorial correspondence analysis and the change of densities of the trophic groups and nematode species indicate that the microfauna partly depends, directly or indirectly, on the presence of litter. In the experimental plot L –, the disappearance of the litter standing on the soil at the beginning of the experiment has been a rapid phenomenon : the soil was uncov-

ered in spring 1987, i.e. approximately 18 months after the beginning of the perturbation. This perturbation, accompanied by structural, climatic and trophic modifications (David *et al.,* 1991; Ponge *et al.,* 1993), seems to have a rapid influence on the nematode fauna. In contrast to the macrofauna and the mesofauna, a change of the nematode population densities is observed from spring 1986 in the surface horizon (0-3 cm) and with a delay of approximately 18 months in the depth levels (– 3-10 cm).

Comparison with a similar experiment on calcic mull, in an oak and hornbeam grove (Arpin *et al.,* 1985), shows an identical response for the depth levels (maintenance or even temporary increase of densities then regression) but apparently an opposite behaviour for the surface levels (increase of densities during the first two years on calcic mull). Moreover, on the two experimental sites, autumn collections are more abundant than spring collections.

In fact the two sites differ by the quantity of organic matter, well incorporated but weakly decomposed in the calcic mull (despite a low C/N, about 11.8; Vannier, 1970) while there is no or little accumulation in the acid mull where the organic matter turnover is rapid (Duchaufour, 1977, 1980). Furthermore, conversely to the acid mull, the calcic mull showed a luxuriant herbaceous layer (*Mercurialis perennis* L. and *Hedera helix* L.), whose death then decomposition after the disappearance of the litter has allowed the installation of a ruderal vegetation type (Umbelliferae, Graminaceae and Compositae) and a temporary nematode fauna increase in the surface layers. In the acid mull, the absence of a herbaceous layer and the low organic matter rate could explain the more important and practically immediate decline of the nematode fauna.

In calcic mull, the maintenance of the densities in depth, or even their temporary increase at the beginning of the experiment, was associated to trophic resources increase, due to the necrosis of the underground vegetative tissues from the herbaceous layer. In the acid mull plot L –, it is more difficult to explain the same nematode fauna behaviour. More simply we can advance a hypothesis : the fine roots of the trees, rather dense and near the surface in the acid humus, would have an identical influence to that the herbaceous layer exerts in the calcic mull (root secretion, activity of the rhizospheric microflora). We can give a relevant element in favour of this hypothesis : in contrast to the other trophic groups, the plant feeder nematodes have an identical behaviour (increase of densities) in the two humus forms, although in the acid mull the increase of these animals is less spectacular and does not last long.

Comparison of the results of these two experiments emphasizes again the importance of the underground vegetative system (herbaceous layer or fine tree roots growing in the surface layers) and its trophic role for the maintenance of the nematode populations. The density of plant cover on the soil and the rhizospheric development that follows it represent an important amount of organic matter for the nematode fauna and must be taken into consideration, for the same reason that the litter is supplied from the canopy, in all soil functional studies. Some analyses support our observations. After clear-cutting in northern Europe coniferous forests, the nematode populations greatly increase their densities (Huhta *et al.,* 1967; Huhta, 1976; Sundman *et al.,* 1978; Sohlenius, 1982); but this phenomenon is transitory and it is followed by a decline. In addition to microclimatic effects, the clear-cutting, according to these authors, entails an important accumulation of pine needles and varied remains on processed plots, as well as death and decay of the root systems. As for the experiment on calcic mull, this entails an increase of the available reserves, in the beginning, and the observed effects in the two cases are similar. The work of Sohlenius (1982) notably tests the influence of these supplies by comparing zones where the remains dwell on the soil and those where they have been removed : in this last case, the nematode densities are lower and they regress with time, the effect being more emphasized in the litter and the humus layer than in the organo-mineral horizon. These results entirely support our observations, but the effects due to the decaying of root systems are not separable from those due to the varied supplies of remains. Litter suppression experiments (a treatment less drastic than clear-cutting because it allows consecutive disorders to the passage to open environments to be got rid of), give complementary information on the importance of the litter and underground vegetative systems on soil nematode populations. Thus, in the acid mull, the change and the different reactions observed between " Surface " and " Depth " levels, also confirm that the soil functions as a double interconnected system (Arpin *et al.,* 1985) : 1 - a surface horizon more dependent on the litter, rain-leachings and the density of the herbaceous plant cover (for litter supplies); 2 - a depth horizon, more dependent on the influence of the underground vegetative systems. In the case of mulls, the leaching of elements and the work of the burrowing animals allow the connection between these two horizons.

Effects of an increase of litter supplies

By the accumulation of organic matter generated, a two-fold annual litter supply is undeniably accompanied by two major effects operating on soil populations :

- an increase of trophic resources;
- a change of microclimatic and chemical conditions.

Although these phenomena are limited here by the duration of the experiment, some behaviours of the nematode fauna must be emphasized given their ecological significance. Compared to the control plot we have observed :

1 - an emphasis of the relative dominance of fungal feeder nematodes compared to bacterial feeder nematodes;

2 - an emphasis of a disparity in the number of nematodes collected on surface (0-1 cm) as compared to the other sampling levels in depth;

3 - correlatively to point 2, a particular behaviour of the level – 1-3 cm, which shows until spring 1987 a change in populations as comparable as that of a surface level (0-1 cm) then similar to that of depth levels (– 3-10 cm);

4 - an increase of the densities of Cephalobidae and *Plectus* sp., in contrast to the other bacterial feeder nematodes.

These four points, if not characteristic of a trend to a soil acidification (Arpin, 1985), at least must be interpreted as significant of an organic matter accumulation, a hyphal dominance litter decomposition and a change of the nematode fauna recalling that observed in a moder or dysmoder humus type. Analogous phenomena have been emphasized (Bassus, 1962; Wasilewska, 1971, 1974; Twinn, 1974) : although the term " soil acidification " has never been truly evoked by these authors, the characteristics of the medium described in these works authorize such an assertion. In any case, similar results are found by Arpin and Ponge (1986) where the physico-chemical analysis of the prospected humus allows no doubt. The importance of the bacterial feeders/fungal feeders ratio as an indication of the mode of litter decomposition has also been emphasized (Böstrom & Sohlenius, 1986; Huhta *et al.*, 1986; Sohlenius *et al.*, 1987, 1988).

The behaviour of the bacterial feeders Cephalobidae and Plectidae is also noteworthy, because on this plot L ++ we find changes previously described : these nematodes increase their densities in rich organic matter environments, being from an intense microbial decomposition (Arpin *et al.*, 1985), or an accumulation of litter as we observe in acid humus like the moder or dysmoder type (Arpin & Ponge, 1986). Ruess and Funke (1992), during experiments of soil acidification, also point out a dominance of the fungal feeder nematodes (*Aphelenchoides* sp.), as well as a sensible increase of densities of *Acrobeloides butschlei*, whose trophic behaviour (grazer bacterial feeder species) is very closely related to Cephalobidae present in our experimental plot, while a global reduction of the nematode fauna is observed. Similar observations are pointed out by Ratajczak *et al.* (1989), and Hyvönen and Persson (1990).

Significant physico-chemical differences exist between plots L + and L ++. Ponge *et al.* (1993) in particular point out a significant increase in carbon content of the level 0-1 cm, but a small increase for the level – 1-3 cm as well as, in depth, a slightly lower pH on L ++. Contrary to the macrofauna and the mesofauna, which, on this plot, would show change in neither specific composition nor abundance, the nematodes live in contact with the soil solution; the changes described above must be taken into consideration since they indicate a trend before the chemical phenomenon could even be truly measured by the classic pedological techniques. Arpin *et al.* (1984) evoke the same problem with Mononchida whose species groups and relative abundances can give the history of a biotope and its acidification under the crown of an old oak tree. Furthermore, as pointed out by David *et al.* (1991), a process of litter accumulation has, however, begun on this plot. It was especially concluded that it was due to " the incapacity of the macrofauna to feed or to remove an additional food supply ", even if we could admit an increase of *i)* the consumption by the microfauna, *ii)* the microbial decomposition and *iii)* the leaching. Except for fungal feeder and some bacterial feeder species, all nematode trophic groups record a decrease of their densities, especially at the depth – 1-3 cm. We can therefore consider (on the basis of densities only, because the biomasses have not been determined) that the activity of nematodes has not been directly increased. Thus, the positive effect that would represent a supplementary litter supply could be counterbalanced, in forest systems, by negative effects due to a greater thickness of the litter layer, especially by toxic chemical factors (polyphenols, organic acids?). In any case, the litter as a food cannot be considered in the acid mull as a limiting factor for the maintenance or development of nematode populations.

Effects of the suppression of rain-leaching arrivals

For a long time the resistance behaviour to a water-deficient environment and the reviviscence of some invertebrates have retained the attention of biologists, not only because of physiological and structural modifications that represent in itself the anhydrobiotic phenomenon, but also by reason of economic (plant feeder nematodes) and ecological implications that it engenders. Namely, nematodes, mainly bacterial feeder and fungal feeder species, play a huge role in the processes of organic matter decomposition owing to the complex relationships that they maintain with the microflora. Many ecosystems have been investigated, but most work concerns normally wet habitats and few analyses have been devoted to xeric systems (Freckman, 1978; Demeure & Freckman, 1981; Whitford *et al.*, 1982; Freckman & Mankau, 1986). Even in these cases, few data exist on specific behaviours, the activity of nematodes being generally and globally understood within the trophic groups.

Although synecological in its purpose, our experiment gives some elements of comparison *in situ*, not only on the resistance behaviour to a deficient hydric regime but especially on the aptitude and speed of species to react when the environmental conditions again become fa-

vourable. Especially, the ascent of the soil moisture in spring 1988 and the corresponding resumption of activity of the nematodes is an element whose ecological significance is interesting to analyze.

Considering the control plot, we observe a decrease of densities about 65 %, but all trophic groups are found at the end of the experiment, at least in depth. Our findings recall earlier observations (Freckman *et al.,* 1977; Norton, 1978; Demeure *et al.,* 1979; Demeure & Freckman, 1981), and we may consider that resistance to desiccation is not the privilege of a particular group of nematodes and that anhydrobiosis occurs in all soils. However, Simons (1973) suggests the existence of different behaviours between species, as well as between the different stages in the same species. Laboratory experiments (Demeure *et al.,* 1979) on *Acrobeloides* sp., *Aphelenchus avenae* and *Scutellonema brachyurum* clearly show a gradation in the response of these three nematode species. Our experiment also reveals behavioural differences. Firstly it concerns the important regression, then the disappearance of the algal feeder and predatory nematodes. Arpin (1969, 1976) pointed out the importance of the hydric stress for the predators Mononchida and the extreme sensitivity of these animals to osmotic pressure variations. Freckman and Mankau (1986) gave a list of species collected in the rhizosphere of various plants in deserts where Mononchida do not appear in the definite omnivorous – predator group either. Furthermore, among the bacterial and plant feeder nematodes, we have observed a gradation between (1) species which rapidly disappear (e.g. *Rhabditis* sp., *Teratocephalus crassidens, Plectus* sp., *Longidorus* sp., *Helicotylenchus pseudorobustus*) (2) resistant species but collected only in low density in deep horizons – 6-10 cm (e.g. *Anaplectus granulosus, Alaimus primitivus, Criconemella* sp., *Diphterophora communis*) and (3) hard resistant species (*Cephalobus persegnis, Paratylenchus* sp., and in a lesser extent *Tylolaimophorus typicus*). In Freckman and Mankau (1986) as in Whitford *et al.* (1982) the only bacterial feeder nematodes found in desert soils also belong to Cephalobidae, and Demeure *et al.* (1979) take into account the high adaptation of *Acrobeloides* sp., to drought. But what appears important in our experiment, is the explosive density of these species (peak in spring 1988), which has a double significance. Firstly, it shows a strong adaptation to dry environments; this adaptation is probably well registered in the genetic patrimony of these species, because they live in our wet temperate region, where forest soils rarely reach saturation deficits beyond the critical threshold of water accessibility, situated for the majority of animals below the wilting point (Vannier, 1971, 1972, 1973). Secondly, these sudden and great increases of density are the sign of a real colonizing capacity. With much prudence Wallwork (1982) suggests that nematodes in desert ecosystems must be " K " strategists by their anhydrobiotic ability and the lack of a tactics of reproduction expressing a varying density. Our experiment, namely the response of Cephalobidae, *a priori* seems to contradict this suggestion. The simulation models of Moorhead *et al.* (1987) also show that the anhydrobiosis, associated with a high capacity of reproduction and a rapid development, maintains the life capacity of these animals in these soils. These findings demonstrate once again the complexity of the interrelations between demographic parameters (here the density) and environmental factors. Unpublished results on the influence of the deforestation in French Guyana showed a significant decrease of the density and diversity of the nematode fauna from the forest itself to the deforested zone, then the deforested and burnt zone; in latter, 95 % of the population were represented by the bacterial feeder nematodes Cephalobidae.

We can, however, raise the question of the ecological significance between this colonizing capacity and the role played by these species in the organic matter decomposition. Arpin *et al.* (1985) had acknowledged, in natural conditions, the existence of successive seasonal waves of maximal activity, according to a regular cycle and concerning not only the trophic groups (succession fungal feeders, bacterial feeders, predators, plant feeders), but also the species within the trophic groups (notably Rhabditidae always precede Cephalobidae). Furthermore Arpin (1985), from experiments on a simple food chain, suggests that a nematode (notably a bacterial feeding species) can colonize a medium only when the former is capable of receiving it. From the above, we could suppose, the hydric component put aside, that different species play, if not the same role, at least an equivalent role in different ecosystems.

In short the effects of manipulating environmental conditions have extended our knowledge on nematode population dynamics.

As sampling strategy may affect perceived pattern of population changes, a regular investigation of the nematode populations is indispensable to all studies dealing with soil biology. Withholding of litter illustrates the importance of roots and rhizosphere processes, particularly marked by the reaction of plant feeding nematodes. With a doubling of litter supplies nematode populations dynamics emphasize soil acidification processes. Interception of rainfall, by drying soil and by influencing resumptions of nematode activity to the only capillary ascent illustrates important specific behavioural differences and the fact that different species can play a similarly role in different ecosystems.

Thus, the efficiency of a system, often attributed to its organization and degree of complexity as well as the functional weight must be attributed to the biodiversity, which requires further field researches.

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